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Increased food provisioning by female Montagu's Harriers in years with food shortage weakens sex-specific roles in parental care

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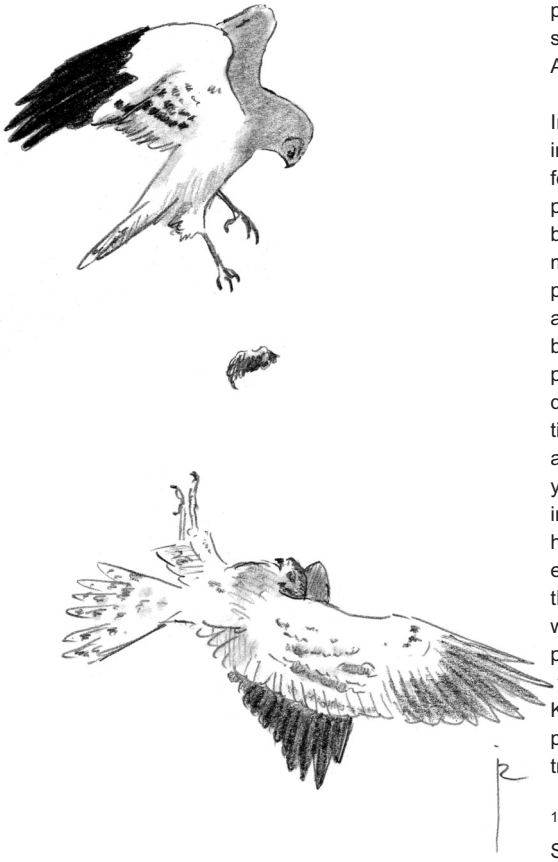

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In many owl and raptor species, sexes have distinct parental roles. Females incubate the eggs and raise the chicks until independence, while males provide females and their chicks with food. This is believed to reduce sexual conflict over parental care as tasks do not overlap. The level of parental care is also shaped by parent-offspring conflict. The scarcity of empirical data on parental investment in species with sex-specific parental roles was our motivation to study parental care in the Montagu's Harrier *Circus pygargus* in relation to natural annual variation in food availability (vole abundance). By tracking individual birds using GPS-trackers, several aspects of parental care (the number of food provisioning trips, home range size and nest attendance) could be quantified for different nesting phases. We found that in food-poor years, males spent less time near the nest, and had lower food provisioning rates during the incubation and nestling phases. In addition, males had larger home ranges in food-poor years, a possible indicator of increased foraging effort. In contrast, females increased their contribution to food provisioning in food-poor years, as shown by higher food provisioning rates and larger home ranges. This increased foraging effort came at the cost of lower nest attendance by females. Our data suggest that, when food abundance declines, Montagu's Harriers shift from a system with almost strict sex-specific parental roles towards a system where both parents provide the same type of care with possibly increased sexual conflict.

Key words: Montagu's Harrier, *Circus pygargus*, biparental care, sex-specific parental roles, food availability, sexual conflict, parent-offspring conflict, GPS-tracking

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In many owl (Strigiformes) and raptor (Falconiformes) species, sexes have distinct parental roles (Andersson & Norberg 1981). Generally, females incubate the eggs and raise the chicks until independence, while males provide females and their chicks with food (Zárybnická & Vojar 2013). A system with sex-specific parental roles is one possible outcome of sexual conflict over biparental care (Barta *et al.* 2014). Such conflicts occur in biparental care systems where both parents benefit if the other parent invests more energy in caring for offspring (Chapman *et al.* 2003, Houston *et al.* 2005). Distinct sex-specific parental roles arise when offspring require two non-interchangeable types of care (e.g. care for the offspring at the nest and food provisioning) and when sexes differ in the costs of performing these tasks (Barta *et al.* 2014).

The level of parental investment is also shaped by parent-offspring conflict over parental care. Parental care promotes fitness of current offspring, but is costly to the parents in terms of increased mortality and reduced future reproduction (Clutton-Brock 1991, Daan *et al.* 1996). This results in a trade-off between

investing energy in current and future reproduction (Harrison *et al.* 2009). Life history theory predicts that in long-lived species such as raptors and owls, with large potential future reproduction, parents should adopt a conservative reproductive strategy and favour their own survival over current reproduction (Erikstad *et al.* 1998).

Theoretical biologists have tried to predict evolutionary stable outcomes of biparental conflicts, and came up with three possible outcomes (as reviewed by Johnstone & Hinde 2006): (1) matching one's effort to that of the other parent, (2) partial compensation, where the better-informed parent will compensate for the reduced parental care of the other parent, and (3) no compensation by the less informed parent. The negotiation model proposed by Johnstone & Hinde (2006) incorporates knowledge on the parental effort of the other parent, the level of care needed by the young and the individual parental states (e.g. the physiological condition of the parents), which in turn determines how one parent should respond to the other's reproductive effort. Reviews on parental investment and sex-specific parental roles emphasize the need for empirical data, to test the assumptions made in theoretical models (e.g. Houston *et al.* 2005).

One would expect that the level of parental care can be influenced by external factors (e.g. environmental conditions such as food availability) as well. However, empirical data on how food availability affects parental care in species with sex-specific parental roles are scarce. This topic has been studied relatively extensively in the Tengmalm's Owl *Aegolius funereus* (e.g. Andersson & Norberg 1981, Eldegard & Sonerud 2010, 2012, Zárybnická & Vojar 2013). In this species, males provide the family with food, whereas females care for the young and generally contribute little to food provisioning (Andersson & Norberg 1981). Experimental supplementary feeding further increased this task specialization (Eldegard & Sonerud 2010). When food was supplemented, both males and females reduced their own provisioning rates, which suggests that they adjust parental investment to one another, indicating a possible sexual conflict over parental care. Supplementary feeding did not benefit offspring, but reduced body mass loss in adults, suggesting that the parents used the increased food supply to reduce the cost of caring for the current offspring rather than producing fitter offspring (Eldegard & Sonerud 2010). Zárybnická & Vojar (2013) studied the effect of natural variation in male food provisioning rate on parental behaviour of female Tengmalm's Owls and found that females adjust their provisioning rate to the investment of their partner and prioritize future reproduction and own survival over the quality of the current offspring. The latter is also indicative of parent-offspring conflict over parental care.

The scarcity of further empirical data on parental investment in species with sex-specific parental roles was our motivation to study parental behaviour in the Montagu's Harrier *Circus pygargus* in relation to natural annual variation in food availability. Just as Tengmalm's Owls, Montagu's Harriers have distinct sex-specific parental roles, in which the female only contributes to food provisioning during the late nestling and fledgling stages (Clarke 1996). In order to further study sex-specific parental roles, male and female harriers were tagged with GPS-trackers (Schlaich *et al.* 2017a), which allowed us to register their movements in detail. From the GPS tracking data, several aspects of parental care, i.e. the number of food provisioning trips, home range size and nest attendance, could be quantified.

We expected that (1a) male food provisioning rates would be higher in food-rich years compared to food-poor years, because of higher foraging efficiency in food-rich years. As a response, we expected that (1b) females would contribute more to provisioning offspring in food-poor years, assuming that the parents adjust parental investment to one another (Johnstone & Hinde 2006, Zárybnická & Vojar 2013). In addition, we expected that (2a) male nest attendance would be higher in food-rich years, as a result of a higher number of food deliveries in food-rich years, and (2b) that female nest attendance would be lower in food-poor years, as a result of a larger number of food provisioning trips by females. Finally, we expected that (3a) male home range size would be smaller in food-rich years compared to food-poor years, because foraging efficiency will be higher when food is abundant, and that (3b) the home range size of females would be larger in food-poor years, due to females increasing their contribution to food provisioning in conditions of lower foraging efficiency.

METHODS

Study species and study area

The Montagu's Harrier is a long-distance migrant with a Palearctic breeding and Afrotropical/ Indomalayan wintering distribution (Clarke 1996, del Hoyo *et al.* 1992, von Blotzheim *et al.* 1989). In The Netherlands, a small but stable breeding population occurs in large-scale agricultural areas in the provinces of Groningen, Flevoland and Friesland (Koks *et al.* 2007, Schlaich *et*

al. 2017b). Here, the harriers nest mainly in crops such as cereals and alfalfa, and therefore nests (and breeding females) need protection from harvesting activities.

The Dutch breeding population heavily relies on voles, mainly Common Vole *Microtus arvalis*. In years when voles are abundant, more harriers attempt to breed, harrier nests contain a higher number of young, and nesting success is higher, which ultimately results in more recruits to the population in subsequent years (Koks *et al.* 2007, Trierweiler 2010). As vole numbers fluctuate in a cyclic way (Cornulier *et al.* 2013), years with high vole abundance alternate with years of low vole abundance. The ecology of Montagu's Harriers breeding in The Netherlands has been studied intensively in order to test and improve measures (i.e. Agri-Environment Schemes) implemented to improve foraging conditions for this red-listed farmland bird (e.g. Klaassen *et al.* 2014, Schlaich *et al.* 2015).

GPS-tracking

To determine the efficiency of conservation measures (e.g. Schlaich *et al.* 2015), 25 male and 9 female Montagu's Harriers were tagged with GPS-trackers (Bouten *et al.* 2013) in 2009–2015, in Eastern Groningen (53.2°N, 7.2°E), the core of the harriers' breeding distribution in The Netherlands. We used this tracking dataset to study parental behaviour of Montagu's Harriers in relation to natural annual variation in vole availability. See Figure 1 for an example of tracking data for a breeding pair.

Montagu's Harriers were captured near the nest either using a mist net in combination with a stuffed Goshawk *Accipiter gentilis* or a snare trap mounted on a perch. Birds were fitted with 12–14 g UvA-BiTS GPS-trackers (Bouten *et al.* 2013, www.uva-bits.nl) using a full-body harness made from 6 mm wide Teflon ribbon strings (Kenward 1987). Birds were released within 20–40 min after capture. We never observed nest desertion or failure in relation to capture events. GPS-trackers were programmed to collect GPS-positions every 5 min between 6:00 and 19:00 GMT, and every hour to two hours during the night. In addition, hourly blocks of high-frequency data (GPS-fixes every 3 seconds) were collected, but these data were subsampled to 5 min for our analysis.

From the tracking data, the daily number of food provisioning trips, daily nest attendance and daily home range size were calculated. Food provisioning trips were identified from the GPS-tracking data, assuming that such trips are characterised by the bird returning to the nest (<250 m from the nest) after having foraged at a certain minimum distance from the nest (>500 m). As females might collect the prey from the male at a considerable distance from the nest (sometimes at >250 m from the nest), an additional set of rules was created to automatically identify trips, where movements in which a bird that approached the nest to within 500 m, after having been foraging far away (>1000 m) from the nest, were also classified as foraging trips. See Figure S1 and Table S1 for a visualization and explanation of the set of rules to identify foraging trips. Nest attendance was defined as the proportion of time per day spent at or near the nest (<250 m from the nest). The daily home range size was calculated as the number of 250×250 m grid cells visited on a certain day (see Klaassen *et al.* 2014).er

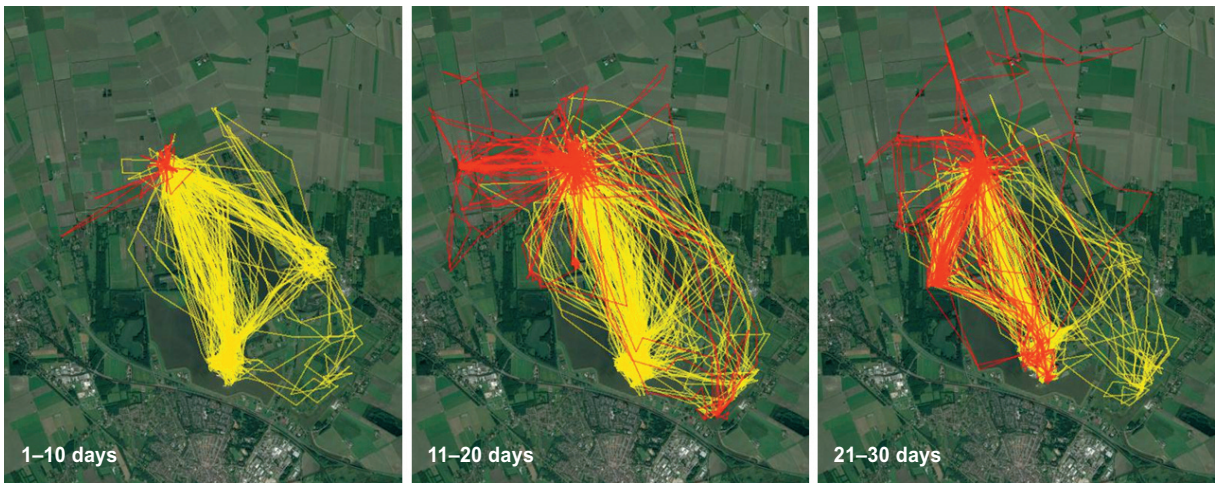

Figure 1. Tracks of a paired male (yellow) and female (red) Montagu's Harrier during the nestling phase, in a year with relatively low vole densities (2012). The nestling phase was subdivided into three 10-day periods. Note that the female started to make longer foraging trips during the second period, i.e. when the young were 11–20 days old.

Male Montagu's Harrier delivering a Common Vole to its breeding female in a typical food pass (photo Rein Hofman, East-Groningen, 22 July 2015).

Several individuals were tracked during multiple breeding seasons. A breeding season during which a particular bird was tracked is referred to as a 'bird year' (thus the data of an individual that was tracked during multiple years contains several bird years). Bird years without breeding or failed breeding were excluded from the analysis. The final dataset contained 43 bird years (for males 20 bird years tracked in food-rich and 12 in food-poor years, for females 4 bird years in food-rich and 7 in food-poor years). See below for the classification of years in food-rich and food-poor.

Food availability

In our population, the Common Vole is the main prey of Montagu's Harriers during the breeding season (Koks *et al.* 2007, Trierweiler 2010). Previous studies have used measures of vole abundance to directly quantify food abundance (e.g. Schlaich *et al.* 2015). For our study area, standardized vole (burrow) counts were only available for 2011–2014 (Table 1). As breeding success of the harriers (brood size) positively correlates with vole abundance (Koks *et al.* 2007, Salamolard *et al.* 2000), we used the annual average brood size (Ottens & Postma, 2014) as a measure to distinguish between food-poor and food-rich years. Average brood sizes in our study population from 2009 to 2015 were 2.4, 1.8, 2.4, 1.4, 1.0, 2.5 and 2.5 young/nest. Based on these data, we assumed that foraging conditions were moderate to good in 2009, 2010, 2011, 2014 and 2015 (food-rich years) and less good in 2012 and 2013 (food-poor years). This subdivision into food-rich and

Table 1. Overview of the mean number of fledglings in Groningen and the vole abundance counted per year (if available) based on Ottens & Postma (2014) and Klaassen *et al.* (2014).

Year	Mean number of fledglings	Vole abundance
2009	2.4	NA
2010	1.8	NA
2011	2.4	5.00
2012	1.4	1.99
2013	1.0	1.96
2014	2.5	7.90
2015	2.5	NA

food-poor years was in line with field observations (i.e. vole counts; see Table 1), with, respectively, 1.99 and 1.96 vole burrows/100 m in 2012 and 2013, and 5.00 and 7.90 vole burrows/100 m in 2011 and 2014 (see Klaassen *et al.* 2014), and with the percentage of alternative prey (mainly songbirds and insects) in harrier pellets (see Koks *et al.* 2001, Schlaich *et al.* 2017b). Average brood size in 2010 (1.8) was intermediate to brood sizes in food-poor (1.0–1.4) and food-rich (2.4–2.5) years. Impressions from the field indicated that 2010 resembled a food-rich year, and hence we decided to consider it as such.

Statistical analyses

The three aspects of parental care, i.e. food provisioning, nest attendance and home range size, were analysed separately in different models within the R Statistical software (v. 3.4.0, R Core Team 2017). Food provisioning trips per day were count data, therefore analysed using a generalized mixed effects model (GLM, lme4 package, v. 1.1–13; Bates *et al.* 2015) with a Poisson distribution (Bolker *et al.* 2008, Zuur *et al.* 2009). Nest attendance were proportional data. Arcsine transforming the nest attendance variable was the most appropriate method to improve the model's fit and was subsequently analysed using a linear mixed effect model (LME, lme4 package). Home range size were count data, but were square root transformed to meet model assumptions and subsequently analysed by a linear mixed effect model. Separate analyses were conducted for males and females, as the raw data plotted in Figure 2 clearly shows that males and females show distinctive behavioural patterns.

Main effects in the full models, i.e. models before model selection, were 'breeding phase' (i.e. incubation period, nestling period, and fledgling period), 'type of year' (food-rich and food-poor year), and 'days' (i.e. the number of days relative to lay date of that specific bird year, centred to overcome scaling issues) and its quadratic component (Crawley 2007). As females stay almost continuously at the nest during the incubation phase, making no foraging trips, models for females only included data for the nestling and fledgling phases. Random factors included were 'individual' and 'year'. Furthermore, we included brood size as a random slope for year, to allow for different slopes per year (following Crawley 2007). During model selection, a simpler model with brood size as main effect was also considered (step 1 & 2 in Table S4). Furthermore, the GLM models included individual observation-level random effects, for males and females separately, to account for over-dispersion. Model selection was done via step-by-step backwards elimination of the full model, for main effects and interactions between type of year and breeding phase, using the anova function (lmerTest package, v. 2.0–33; Kuznetsova *et al.* 2016) until a model was obtained that only included significant predictors and which had the lowest Akaike Information Criterion (AIC) score (see Tables S4–7 for more details).

RESULTS

Individuals showed large day-to-day as well as between-individual variation in the number of food provisioning trips, nest attendance and home range size, but nevertheless some distinct seasonal patterns and differences between sexes were found (Figure 2).

Food provisioning trips

Females only started to make food provisioning trips after the incubation phase, and thus the number of food provisioning trips increased with every breeding phase (Figure 2A). Females made more food provisioning trips in food-poor compared to food-rich years (Table 2, Figure 3A, $z = -2.510$, $P = 0.012$). In addition, a significant interaction between type of year and breeding phase was found ($z = -2.246$, $P = 0.025$; see Tables S3 and S8A for details), supposedly because the increase in the number of food provisioning trips between the nestling and the fledgling phase was stronger in food-poor years (Figure 3A).

In males, food provisioning trips peaked during the nestling phase (Figure 2A). Males responded to variation in food abundance in the opposite way; they tended to make fewer food provisioning trips in food-poor years compared to food-rich years, at least during the incubation and nestling phase – for the fledgling phase males made more trips in food-poor compared to food-rich years (Figure 3A). This difference between the breeding phases reflected in the fact that overall 'type of year' was not significant (Table 2, Figure 3A, $z = 1.262$, $P = 0.207$), but we did find a significant interaction between type of year and breeding phase ($\chi^2_2 = 16.9$, $P < 0.001$; see Tables S3, S8B and S9 for details).

Nest attendance

In females, nest attendance was nearly 100% during the incubation phase, and this gradually decreased throughout the nestling and fledgling phase (Figure 2B). Nest attendance was lower in food-poor years, but only for the nestling phase (Figure 3B). For the fledgling phase, nest attendance was higher in food-poor

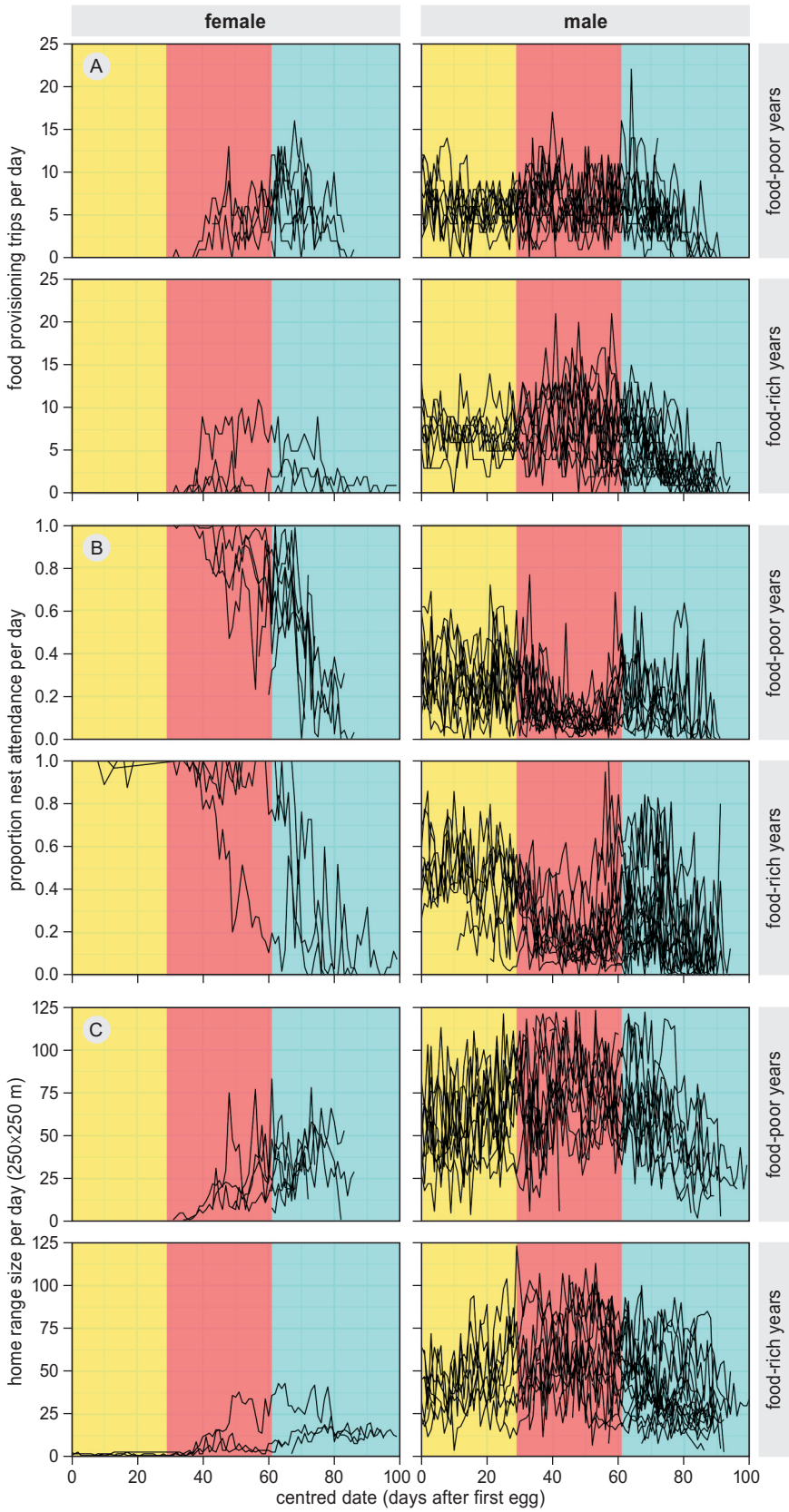

Figure 2. The effect of food availability on (A) food provisioning trips, (B) proportion of nest attendance, and (C) home range size, per breeding phase and per sex. Background colours correspond to different breeding phases (yellow: incubation phase; red: nestling phase; blue: fledgling phase). Each line represents a bird year.

years (Figure 3B). There was a significant interaction between type of year and breeding phase (Table 2, Figure 3B, $t = -2.165$, $P = 0.032$) as the drop in nest attendance between the nestling and fledgling phase was stronger in food-rich years (Figure 3B). Overall, type of year was not significant ($t = -1.133$, $P = 0.898$; see Tables S3 and S10A for details).

Male nest attendance varied during the breeding season and seemed lower during the nestling phase (Figure 2B). Nest attendance was lower during food-poor years compared to food-rich years (Table 2, Figure 3B, $t = 4.331$, $P = 0.014$; see supplementary Tables S3 and S10B for details).

Home range size

Female home range size generally increased during the breeding season (Figure 2C). Home range size was significantly larger in food-poor years compared to food-rich years (Table 2, Figure 3C, $t = -5.224$, $P < 0.001$). Furthermore, a significant interaction between type of year and breeding phase was found ($t = -2.001$, $P = 0.047$), presumably because the difference between food-poor and food-rich years was greater during the fledgling phase compared to the nestling phase (see Tables S3 and S11A for details).

The home range size of males peaked during the nestling phase (Figure 2C). Just as in females, home range size was larger in food-poor years compared to food-rich years (Table 2, Figure 3C, $t = -7.479$, $P < 0.001$). Finally, an interaction between type of year and breeding phase was found ($\chi^2_2 = 13.0$, $P = 0.002$; see Tables S3, S11B and S12 for details), probably because the increase in home range size during the nestling phase was more prominent in food-poor years (Figure 3C).

DISCUSSION

Natural variation in food abundance affects parental care in Montagu's Harriers in a similar way to that seen in Tengmalm's Owls (Zárybnická & Vojar 2013); in years with low vole numbers (food-poor years), males seem to decrease and females to increase their contribution to food provisioning.

Why would males contribute less to food provisioning in food-poor years? A first obvious explanation is that food was limited and thus that males could not manage to find more food. Male Montagu's Harriers have been shown to increase their food provisioning with increased brood size, but are limited by vole abundance (Arroyo *et al.* 2002). This has also been shown for the Common Kestrel *Falco tinnunculus* in an experimental setup (Daan *et al.* 1996), thus male raptors

Table 2. Overview of the minimal adequate models (MAMs) for each response variable (i.e. food provisioning trips, nest attendance and home range size) for each sex and the difference between food-poor and food-rich years. Effects highlighted in bold represent the most important effects for the current study.

Response variable	Sex	Model	Food-poor vs rich-food years
Food provisioning trips (GLMM)	Female	Food provisioning trips ~ centred days from lay date + centred days from lay date² + **breeding phase × type of year** + (1 | bird year) + (brood size | year) + (1 | observation count)	>
	Male	Food provisioning trips ~ centred days from lay date + centred days from lay date² + **breeding phase × type of year** + (1 | bird year) + (brood size | year) + (1 | observation count)	**No significant effect of type of year**
Nest attendance (LMM)	Female	Arcsine √nest attendance ~ days from lay date + days from lay date² + **breeding phase × type of year** + (1 | bird year) + (brood size | year)	**No significant effect of type of year**
	Male	Arcsine √nest attendance ~ centred days from lay date + centred days from lay date² + **breeding phase + type of year** + (1 | bird year) + (brood size | year)	<
Home range size (LMM)	Female	√Home range size ~ centred days from lay date + centred days from lay date² + brood size + **breeding phase × type of year** + (1 | bird year)	>
	Male	√Home range size ~ centred days from lay date + centred days from laydate² + **breeding phase × type of year** + (1 | bird year) + (brood size | year)	>

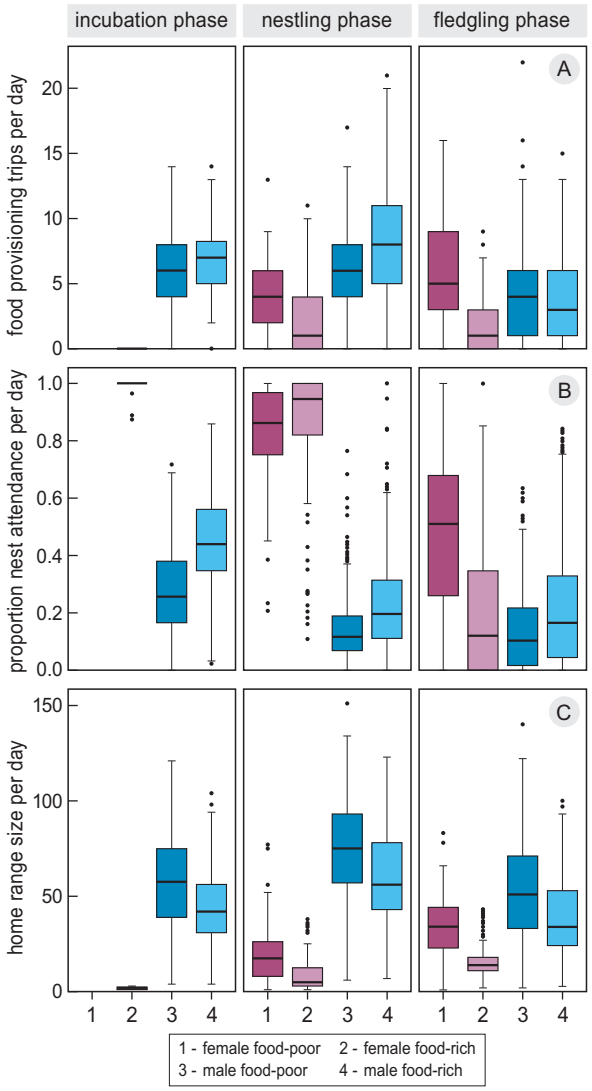

Figure 3. The effect of food availability on (A) food provisioning trips, (B) proportion of nest attendance, and (C) home range size, per sex and type of year, for each breeding phase. Shades of pink represent females, shades of blue males. Darker shades are the food-poor years, lighter shades are the food-rich years.

seem to be able to adjust provisioning rates to some extent. Indeed, home ranges of the males were larger in food-poor years, suggesting that males increased their foraging effort, but this might have still been insufficient to compensate for the decrease in food availability. An alternative explanation is that males chose to decrease their provisioning efforts. This could be the result of an intensified parent-offspring conflict (i.e. males choose to invest less in less-fit offspring, prioritizing own survival and future reproduction over current reproduction). Alternatively, it could also be a result of an intensified sexual conflict where males reduce their own share at the cost of increased female effort, prioritizing own condition and survival over the condition and survival of their partner. Based on the current data, it is impossible to say whether a constraint in food availability or an intensified parent-offspring or sexual conflict causes a reduction in food provisioning in males. Experiments, such as food provisioning trials, would be needed to discern between these different hypotheses (Zárybnická & Vojar 2013). In addition, information on the condition of the adult birds as well as the chicks would be needed to be able to determine how family conflicts are played out (see Eldegard & Sonerud 2010).

We have anecdotal evidence that males are willing to invest less in their current brood in food-poor years from our catching efforts. It was much more difficult to capture males for our GPS-tracking studies in food-poor years as they were less aggressive towards the stuffed Goshawk that we used to lure the birds into the mist net. Although we did not formally quantify capture rates, the difference between food-poor and food-rich years was striking. This observation makes it more likely that males would be physically and physiologically able to provide more food items, but that they choose not to do so because of either parental-offspring or sexual conflict. Arroyo *et al.* (2017) suggested that females are also willing to invest more in nest defence in food-rich years, based on the reaction of harriers to human intruders.

Why do females increase their provisioning effort in food-poor years? The increase in provisioning effort by females is likely to be a direct response to the decreased effort of the males, strongly suggesting the existence of a sexual conflict over food provisioning in Montagu's Harriers. The theoretical model by Johnstone & Hinde (2006) assumes that what they called the focal parent (i.e. the parent who spends most time near the nest and cares for the young) is most effective at adjusting parental investment as it receives the most information. In Montagu's Harriers, the female is the better-informed parent, because she probably knows the food requirements of the offspring and the amount of provisioning provided by the male, thus females may be more likely to adjust provisioning efforts than males. However, whether male provisioning efforts dictate female provisioning efforts, or the other way around, remains to be established. This could be investigated by experimental work such as food provisioning experiments.

One of the consequences of the increase in food provisioning effort of females is that their nest attendance decreased, i.e. females left their nests unguarded

for longer time. This behavioural change could contribute to an increased predation rate and thus lower nest success of Montagu's Harriers in food-poor years. However, the exact relationship between nest attendance time and predation rates still needs to be established.

What are the implications of variation in food abundance on the sex-specific parental roles and the sexual conflict on food provisioning in Montagu's Harriers? Our data show that in food-poor years a shift occurs from more sex-specific parental roles towards male and female parents having similar roles. It is likely that this increases the conflict between sexes over parental care, and therefore we would expect that the provisioning effort of females in food-poor years is more strongly tuned to the provisioning effort of their male partner, whereas in food-rich years foraging efforts of males and females might not be related to each other. It would be interesting to relate the provisioning effort of one parent to the other, in food-poor and food-rich years (Johnstone & Hinde 2006). For this, it would be required that both parents of a nest would be tagged with a GPS-tracker. Although we occasionally specifically targeted the partner of a tagged bird, only in one case could a tagged pair be followed throughout the whole breeding season (see Figure 1).

Females increased nest attendance in food-poor years during the fledging period, whereas nest attendance was lower in food-poor years during the nestling period. This difference might be an artefact caused by the fact that Montagu's Harriers have a shorter fledging period when food is abundant, whereupon females leave the brood at an earlier stage compared to food-poor years (see Arroyo *et al.* 2002). This is believed to mainly affect nest attendance time.

To conclude, food scarcity does seem to weaken the sex-specific parental roles in Montagu's Harriers, which possibly increases the strength of sexual conflict. Our results also suggest that the energetic costs increase for both males and females in food-poor years (i.e. males have larger home ranges, females make more provisioning trips), thus parents of both sexes seem to increase their own investment. At the same time, reproductive output decreases (young are in a poorer condition and nest predation risk is higher because of a shorter nest recess time in females), thus the increase in effort by parents appears not to compensate for the reduction in food availability; this might be the outcome of parent-offspring and sexual conflicts over parental care. Future research, such as food provisioning experiments, but also evaluations of the relative contribution of males and females from the same nest, are required to further elucidate the drivers behind parent-offspring and sexual conflicts in the Montagu's Harrier and their importance for shaping sex-specific parental roles in general.

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SAMENVATTING

Bij roofvogels en uilen zien we vaak een duidelijke rolverdeling tussen de seksen: de vrouwtjes bebroeden de eieren en zorgen voor de jongen, terwijl de mannetjes voor het voedsel zorgen. Het idee is dat dit een van de manieren is om een conflict tussen de seksen over de zorg voor de jongen uit de weg te gaan. Ook wordt de mate van ouderlijke zorg vormgegeven door het conflict tussen ouders en hun jongen. Het gebrek aan empirische gegevens over ouderlijke investering bij soorten met een specifieke verdeling van ouderlijke taken tussen beide geslachten was onze motivatie om dit bij de Grauwe Kiekendief *Circus pygargus* in relatie tot de natuurlijke variatie in voedselbeschikbaarheid (in ons geval de dichtheid aan Veldmuizen *Microtus arvalis*) na te gaan. We gebruikten voor deze analyse een grote dataset van kiekendieven die gevolgd waren met GPS-loggers, waaruit we verschillende aspecten van ouderlijke zorg konden afleiden (aantal voedselvluchten, tijd die bij het nest werd doorgebracht, grootte 'home range'). Mannetjes leken in jaren met weinig voedsel minder aan de voedselvoorziening bij te dragen, gezien het feit dat ze minder tijd bij het nest doorbrachten en minder voedselvluchten maakten (tenminste in de broedfase en in de periode met nestjongen). Wel leken ze harder te werken gezien hun grotere 'home ranges'. Vrouwtjes bleken daarentegen juist meer bij te dragen aan de voedselvoorziening in jaren met weinig muizen door zelf meer te gaan foerageren, wat ten kostte ging van de tijd die ze bij het nest doorbrachten. Wanneer het voedselaanbod afneemt, treedt er bij Grauwe Kiekendieven dus een verschuiving op in de rolverdeling tussen de seksen (meer op elkaar lijkend). Hierdoor neemt waarschijnlijk het conflict over ouderlijke zorg tussen de seksen toe.

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SUPPLEMENTARY MATERIAL

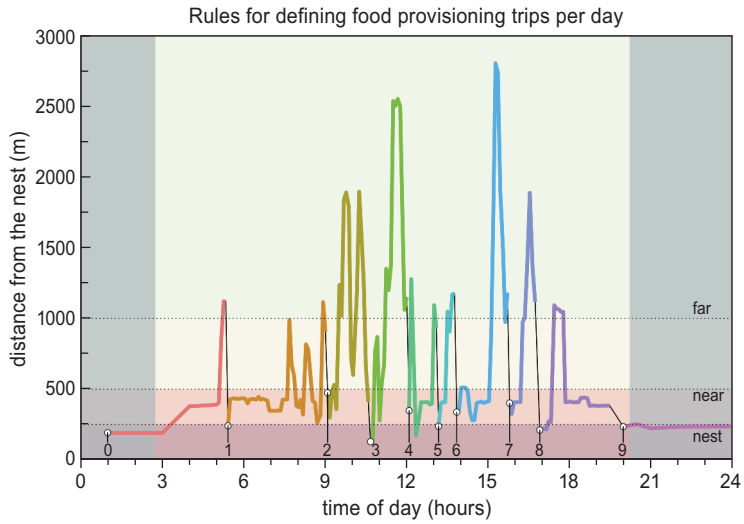

Figure S1. Graph visualizing the set of rules to determine food provisioning trips per day per individual (in this case Edwin, food provisioning measured on 6 May 2014). Horizontal dashed lines indicate thresholds of distance to the nest: in the red zone the bird is at nest (<250 m), orange zone near the nest (250–500 m), yellow zone mid nest (500–1000 m) and green zone far from the nest (>1000 m). The rules are explained in Table S1 in detail.

Table S1. Overview of all the rules for defining food provisioning trips.

Rule	Description	Corresponding number in graph
1	No trips counted during sundown	Trip 9 counts, as it is just before sundown
2	When the distance to the nest is less than 250 m, it counts as a trip	Trip 1, 3, 5, 8, and 9
3	When the distance to the nest changes from more than 1000 m to 500 m but no closer to the nest, it also counts as a trip	Trip 2, 4, 6, and 7
4	When the nest (<250 m) is reached from a distance under 500 m, that does not count as a trip	Just before trip 2 is reached
5	Trips must be at least 2 data points apart to count as separate trips	Just after trip 4 was made; too little time before reaching the nest again, therefore, it does not count as a trip

Table S2. List and description of all the variables of the dataset used for the statistic models.

Variable	Abbreviation	Type	Description
Food provisioning trips	Trip.count	Integer	Response variable; number of food provisioning trips per day
Nest attendance	Na	Numeric	Response variable; Arcsine(√x) transformed nest attendance; proportion of the time per day spend at/near nest (limit set at 500 m)
Home range size	Shrs	Integer	Response variable; Square root transformed Home Range Size. Number of different 250×250m cells counted for the location of the bird
Days (scaled)	Ldz	Numeric	Days counted since egg laying date, centred with scale function to (count.ld-mean(count.ld))/SD(count.ld)
Type of year	Type.year	Factor	Year categorized into 2 levels corresponding with the food availability (poor/rich) of that given year
Breeding phase	Br.phase	Factor	Date categorized into 3 levels according to breeding phase (Incubation phase/ Nestling phase/ Fledgling phase)
Individual	ID	Factor	Names of the individual birds, factor with 29 levels
year	Year.r	Integer	Years of measurement transformed into R-friendly years (1900 = year.r)
Brood size	BS	Integer	Brood Size of the nest corresponding to the bird year
Observations	Obs/obsf	Integer	Function for the number of rows/observations per dataset

Table S3. Overview of the means of all response variables per phase of the breeding season for food-rich or food-poor years per sex. NA means data not available.

		Food-poor years			Food-rich years		
		incubation	Nestling	Fledgling	Incubation	Nestling	Fledgling
Food provisioning (#)	Male	5.9	6.3	4.2	6.9	7.9	3.8
	Female	NA	3.9	6.0	0	2.4	1.9
Nest attendance (%)	Male	0.28	0.15	0.14	0.45	0.23	0.22
	Female	NA	0.83	0.47	0.99	0.84	0.24
Home range size (#)	Male	58.4	75.7	53.7	44.7	58.4	39.6
	Female	NA	19.6	34.6	1.65	9.01	16.5

Table S4. Description of every step in the model selection.

Step in model selection	Changes relative to full model
Full model	Main effects: centred days after lay date and its quadratic term, type of year, breeding phase. Random effects: individual bird years, years with a random slope of brood size. Additionally, for food provisioning a random effect of observations.
1	Simplification of (BS|year.r), BS as main effect, leaving year as (1|year.r)
2	Simplification of (BS|year.r), BS as main effect, leaving year out of the model
3	Simplification of the main effect, continuing with the best random simplification (model full, 1, or 2) and removing the interaction
4	Simplification of the main effect, continuing with the best random simplification (model full, 1 or 2) and removing most non-significant fixed effect

Table S5. Overview of the model selection for food provisioning trips per sex. Per model the degrees of freedom (*df*) and the Akaike Information Criterion (AIC) are noted. Grey background shows the minimal adequate model (MAM) per sex and the factors in bold represent the changes in the model relative to the full model.

Model	Factors included in model	*df*	AIC
A. Female			
Full	ldz + ldz^2 + br.phase × type.year + (1|ID) + (BS|year.r) + (1|obsf)	11	773.04
1	**BS** + ldz + ldz^2 + br.phase × type.year + (1|ID) + **(1|year.r)** + (1|obsf)	10	774.81
2	**BS** + ldz + ldz^2 + br.phase × type.year + (1|ID) + (1|obsf)	9	781.78
B. Male			
Full	ldz + ldz^2 + type.year × br.phase + (1|ID) + (BS|year.r) + (1|obs)	13	9100.90
1	**BS** + ldz + ldz^2 + type.year × br.phase + (1|ID) + **(1|year.r)** + (1|obs)	12	9145.40
2	**BS** + ldz + ldz^2 + type.year × br.phase + (1|ID) + (1|obs)	11	9246.30

Table S6. Overview of the model selection for arcsine transformed nest attendance per sex. Per model the degrees of freedom (*df*) and the Akaike Information Criterion (AIC) are noted. Grey background shows the minimal adequate model (MAM) per sex and the factors in bold represent the changes in the model relative to the full model.

Model	Factors included in model	*df*	AIC
A. Female			
Full	ldz + ldz^2 + br.phase × type.year + (1|ID) + (BS|year.r)	11	34.02
1	**BS** + ldz + ldz^2 + br.phase × type.year + (1|ID) + **(1|year.r)**	10	34.47
2	**BS** + ldz + ldz^2 + br.phase × type.year + (1|ID)	9	43.23
3	**ldz** + br.phase × type.year + (1|ID) + (BS|year.r)	9	34.57
B. Male			
Full	ldz + ldz^2 + type.year × br.phase + (1|ID) + (BS|year.r)	13	–849.41
1	**BS** + ldz + ldz^2 + type.year × br.phase + (1|ID) + **(1|year.r)**	12	–834.62
2	**BS** + ldz + ldz^2 + type.year × br.phase + (1|ID)	11	–820.91
3	ldz + ldz^2 + **type.year + br.phase** + (1|ID) + (BS|year.r)	11	–852.63

Table S7. Overview of the model selection for sqrt-transformed home range size per sex. Per model the degrees of freedom (*df*) and the Akaike Information Criterion (AIC) are noted. Grey background shows the minimal adequate model (MAM) per sex and the factors in bold represent the changes in the model relative to the full model.

Model	Factors included in model	*df*	AIC
A. Female			
Full	ldz + ldz^2 + type.year × br.phase + (1|ID) + (BS|year.r)	11	573.87
1	**BS** + ldz + ldz^2 + type.year × br.phase + (1|ID) + **(1|year.r)**	10	568.85
2	**BS** + ldz + ldz^2 + type.year × br.phase + (1|ID)	9	566.85
B. Male			
Full	ldz + ldz^2 + type.year × br.phase + (1|ID) + (BS|year.r)	13	6491.20
1	**BS** + ldz + ldz^2 + type.year × br.phase + (1|ID) + **(1|year.r)**	12	6520.60
2	**BS** + ldz + ldz^2 + type.year × br.phase + (1|ID)	11	6730.70

Table S8. Overview of the MAM summary for food provisioning trips. In bold are the results representing the differences between food-poor and food-rich years.

FOOD PROVISIONING Variable	Estimate	SE	*Z*-value	*P*-value
A. Female intercept	1.1529	0.1207	9.554	<0.001
Date				
Ldz	0.9867	0.2201	4.483	<0.001
Ldz²	–1.3648	0.1631	–8.368	<0.001
Type year				
Food-poor				
Food-rich	**–0.6064**	**0.2416**	**–2.510**	**0.012**
Breeding phase				
Nestling phase				
Fledgling phase	0.3388	0.1660	2.040	0.041
Interactions				
Rich : Fledgling	–0.4850	0.2159	–2.246	0.025
B. Male intercept	1.42340	0.10847	13.122	<0.001
Date				
Ldz	–0.67284	0.03317	–20.283	<0.001
Ldz²	–0.30667	0.01800	–17.036	<0.001
Type year				
Food-poor				
Food-rich	**0.14883**	**0.11794**	**1.262**	**0.21**
Breeding phase				
Incubation phase				
Nestling phase	0.23665	0.05971	3.964	<0.001
Fledgling phase	0.77403	0.08620	8.980	<0.001
Interactions*				
Rich : Nestling	0.06359	0.05521	1.152	0.249
Rich : Fledgling	–0.16705	0.06385	–2.616	0.009

*See Table S9 for the overall interaction between type of year and breeding phase

Table S9. Male food provisioning trips, overall interaction between type of year and breeding phase.

Model	*df*	AIC	LogLik	Chisq Chi	*df*	P_r (>Chisq)
Full	13	9100.9	–4545.9	16.862	2	<0.001
Without interaction	11	9173.3	–4537.4			

Table S10. Overview of the MAM summary for arcsine transformed nest attendance. In bold are the results representing the differences between food-poor and food-rich years.

NEST ATTENDANCE Variable	Estimate	SE	*df*	*t*-value	*P*-value
A. Female intercept	1.21576	0.06023	6.83898	20.186	<0.001
Date					
Ldz	–0.49895	0.06425	183.45158	–7.766	<0.001
Ldz²	–0.06615	0.04014	182.90793	–1.648	0.101
Type year					
Food-poor					
Food-rich	**–0.01260**	**0.09447**	**6.74203**	**–0.133**	**0.898**
Breeding phase					
Nestling phase					
Fledgling phase	0.09866	0.07033	185.00651	1.403	0.162
Interactions					
Rich : Fledgling	–0.17800	0.08221	183.01875	–2.165	0.032
B. Male intercept	0.44375	0.03977	22.83294	11.159	<0.001
Date					
Ldz	–0.17630	0.01203	1915.72057	–14.653	<0.001
Ldz²	–0.05833	0.00615	1918.61140	–9.484	<0.001
Type year					
Food-poor					
Food-rich	**0.13038**	**0.03010**	**3.79096**	**4.331**	**0.0139**
Breeding phase					
Incubation phase					
Nestling phase	–0.09396	0.02279	1913.47069	–4.122	<0.001
Fledgling phase	0.11359	0.03238	1911.35724	3.508	<0.001

Table S11. Overview of the MAM summary for sqrt-transformed home range size. In bold are the results representing the differences between food-poor and food-rich years.

HOME RANGE SIZE Variable	Estimate	SE	*df*	*t*-value	*P*-value
A. Female intercept	3.22831	0.33223	17.80668	9.717	<0.001
Date					
Ldz	2.37183	0.26294	183.05041	9.020	<0.001
Ldz²	–1.02812	0.16183	177.19374	–6.353	<0.001
Brood size	0.65830	0.11001	107.96587	5.984	<0.001
Type year					
Food-poor					
Food-rich	**–1.97906**	**0.37884**	**49.16095**	**–5.224**	**<0.001**
Breeding phase					
Nestling phase					
Fledgling phase	0.05483	0.29112	184.95470	0.188	0.851
Interactions					
Rich : Fledgling	–0.70346	0.35158	182.70085	–2.001	0.047
B. Male intercept	8.87755	0.32861	76.55085	27.015	<0.001
Date					
Ldz	–0.63374	0.07962	1909.07342	–7.959	<0.001
Ldz²	–0.58350	0.04075	1912.38060	–14.318	<0.001
Type year					
Food-poor					
Food-rich	**–3.68578**	**0.49284**	**31.53006**	**–7.479**	**<0.001**
Breeding phase					
Incubation phase					
Nestling phase	0.78921	0.16764	1914.40162	4.708	<0.001
Fledgling phase	0.64639	0.23159	1911.20379	2.791	0.005
Interactions*					
Rich : Nestling	–0.53979	0.15487	1916.58035	–3.486	<0.001
Rich : Fledgling	–0.46911	0.16412	1923.43763	–2.858	0.004

*See Table S12 for the overall interaction between type of year and breeding phase

Table S12. Male home range size, overall interaction between type of year and breeding phase.

Model	*df*	AIC	LogLik	Chisq Chi	*df*	P_r (>Chisq)
Full	13	6491.2	–3232.6	12.973	2	0.002
Without interaction	11	6500.2	–3239.1			